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ABUNDANCE OF INVASIVE, NON-NATIVE RIPARIAN HERBS IN RELATION TO RIVER REGULATION

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ABSTRACT

River regulation is associated with vegetation encroachment and invasions of some non-native species in the semi-arid west. Shifts in the abundance of native and non-native woody riparian species are an interplay of regulation, life history traits and an array of flow and physical environmental variables. We sought to compare plant densities and per cent cover of several invasive species over two time periods in a paired river study, contrasting three different degrees of regulation along reaches of the Green and Yampa rivers in Colorado and Utah, USA. We censused patches of non-native plants and recorded per cent cover in quadrats along 171 river km. The upper Green (10.1 patches ha⁻¹) had the highest invasive plant patch density followed by the lower Green (4.4 per ha) and the Yampa (3.3 per ha). Invasive species were present in 23%, 19% and 4% of sample quadrats, and an average of 0.28, 0.22 and 0.04 invasive species detected per square metre was recorded along the upper Green, lower Green and Yampa Rivers, respectively. Most species had significantly ($p \leq 0.02$) higher percent cover on the upper Green than either or both the lower Green and the Yampa River. Whereas the less regulated river reaches maintain lower densities of invasive species than the most regulated reach, long-term persistence of this pattern is still in question as some species patches showed notable increases on the Yampa and lower Green Rivers from 2002–2005 to 2010–2011. Although invasion is enhanced by flow regulation, life history traits of some species suggest invasion is likely, regardless of flow regulation. Published 2015. This article is a U.S. Government work and is in the public domain in the USA

KEY WORDS: invasive plants; *Tamarix*; river regulation; Green River; Yampa River; *Cirsium arvense*; *Lepidium latifolium*; *Melilotus officinalis*

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INTRODUCTION

Compared with adjacent uplands, riparian ecosystems display relatively high percentages of non-native or exotic plant species, and these ecosystems, across a broad geographical range, may be inherently vulnerable to invasions by non-native species. Frequent flood disturbance, high edge to area ratios, high longitudinal connectivity, availability of moisture and nutrients are cited as factors contributing to the invasibility of riparian ecosystems (Planty-Tabacchi *et al.*, 1996; Hood and Naiman, 2000; Tickner *et al.*, 2001). Further, fundamental changes in the natural disturbance regime of these systems are thought to favour non-native species (Planty-Tabacchi *et al.*, 1996). A wide array of human-derived disturbances influences riparian ecosystems, across spatial and temporal scales, leading to increases in non-native plants in riparian zones worldwide. Changes in species composition may further drive changes in structure and functioning of riparian ecosystems or have little

effect (Richardson *et al.*, 2007). For our purposes, an invasive plant is defined as a non-native (alien) species, which becomes established and persists in natural or semi-natural ecosystems or habitats, modifies plant species assemblages, is viewed as a problem and may threaten native biological diversity by altering physical and biotic processes (IUCN [International Union for the Conservation of Nature] 1999; Tickner *et al.*, 2001).

Given that fluvial disturbances or changes in the disturbance regime appear to play a key role in non-native plant invasions of riparian zones, it is important to recognize the extent to which stream flows have been modified by human activities. Flows along the majority of large rivers in the northern hemisphere are modified by dams, diversions or other flood control structures (Dynesius and Nilsson, 1994). In the Colorado River basin, the ratio of total reservoir storage volume to mean annual discharge is the largest in North America (Graf, 1999). Dams alter riparian plant communities by changing flood timing, magnitude and duration, which in turn alter fluvial disturbance processes, vegetation patch structure and species composition (Stromberg *et al.*, 2007a). This can lead to vegetation encroachment and channel narrowing (Friedman *et al.*, 1998; Allred and Schmidt, 1999) and typically limits the recruitment of some native plant species (Scott *et al.*, 1996;

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Stromberg 1997; Sher *et al.*, 2000; Dewine and Cooper, 2007). Once established, some invasive species form monotypic stands through interspecific competition, and such stands, particularly for woody species, can alter local fluvial geomorphic processes (Tickner *et al.*, 2001; Manners *et al.*, 2014). Because flow modification is so pervasive, it is often difficult to establish a clear cause and effect relationship between changes in flow and plant invasions in riparian zones.

Flow modification, including reduced peak flows, was shown to produce declines in native riparian species and increases non-native, weedy species, which are more competitive under drier conditions (Catford *et al.*, 2011). However, studies of woody riparian species suggest broad-scale invasion processes are not strictly a function of flow regulation but are best understood as the interplay of the life history traits of the invading species with aspects of the flow regime and catchment characteristics (Mortenson and Weisberg, 2010). For example, tamarisk (*Tamarix* spp. and hybrids) and Russian olive are now the third and fourth most abundant woody riparian taxa in the western USA (Friedman *et al.*, 2005). Studies suggest that the widespread abundance of tamarisk in riparian systems throughout western North America is partially due to flow regulation (Shafroth *et al.*, 1998; Stromberg *et al.*, 2007b; Nagler *et al.*, 2011). Tamarisk also can establish along largely unregulated rivers in certain hydrogeomorphic settings (Birken and Cooper, 2006; Manners *et al.*, 2014) or in response to climate-related changes in streamflow (Allred and Schmidt, 1999). In a study examining 13 perennial rivers spanning a gradient of flow regulation, Merritt and Poff (2010) concluded that whereas tamarisk recruitment was successful across a broad range of flow conditions, adult tamarisk were most abundant at moderate levels of flow modification and dominance was highest on the most heavily regulated rivers. In a similar regional analysis, Mortenson and Weisberg (2010) found that tamarisk cover was positively related to a number of flow variables and to an index of flow alteration. By contrast, Russian-olive cover was unrelated to flow regulation or the degree to which flows were altered. Russian olive has established extensively along both regulated and largely unregulated river systems across the southwestern USA including Canyon de Chelly (Reynolds *et al.*, 2014) and the Escalante River (Webb *et al.*, 2007, M. Scott, unpublished data). These regional studies emphasize the notion that river regulation alone does little to explain the invasion of riparian ecosystems by non-native, woody species. Rather, the life history strategies of native and non-native species should be linked to specific aspects of the flow regime (Mortenson and Weisberg, 2010). This should apply to herbaceous species as well, although there is less direct evidence presented in the literature.

Catford and Jansson (2014) examine life history traits and community assembly rules to examine how adaptations to dispersal, inundation and fluvial disturbance shape riparian communities, including the invasion of non-native species.

They suggest that non-native plants in regional species pools that have successfully invaded riparian ecosystems display a range of dispersal mechanisms, including by water and human activities. We surveyed regionally important weed species at two points in time, along three proximal river reaches with different levels of flow regulation, to assess the spatial and temporal abundance patterns of these invasive, non-native species. These patterns were examined in the context of key life history traits that have been documented for these species.

Within Dinosaur National Monument (NM) (CO and UT, USA), the highly regulated upper Green River, the largely unregulated Yampa River and the less regulated Green River, below the Yampa River confluence, offer a unique opportunity to study the effects of different degrees of flow regulation on riparian ecosystems where pre-development flows and geomorphic setting and vegetation were similar (Merritt and Cooper, 2000). In similar bedrock canyon settings and across three degrees of flow regulation, our specific objectives were the following: (1) to census for patches of priority invasive, non-native weeds within Dinosaur NM, Colorado and Utah; (2) to quantitatively compare the relative frequency and cover of these species; (3) to compare any changes in absolute numbers and patch sizes of these priority non-native plant species between two sampling periods (from 2002–2005 to 2010–2011) and (4) to examine these results in the context of life history traits that are relevant to dispersal, establishment and persistence in these riparian environments.

METHODS

Study area

A 33-km reach of the Green River through Lodore Canyon, the lower 76 km of Yampa River to its confluence with the Green River and 62 km of the Green River below this confluence occupy deep, bedrock canyons and are contained within Dinosaur NM where both rivers incise the eastern flanks of the Uinta Mountains (Figure 1). The Green River above the confluence with the Yampa River (upper Green) has been highly regulated since Flaming Gorge Dam was completed in 1962. Conversely, in spite of a small main stem reservoir, agricultural diversions and tributary reservoirs, the Yampa River retains a mean annual discharge and peak flow near historic values (Andersen *et al.*, 2007). Below the confluence of these two contrasting reaches, flows of the Green River (lower Green) can be considered partially restored as it receives inflows from the Yampa. Both rivers above the confluence have approximately the same mean annual flow volume, similar-sized watersheds and historically featured a snowmelt spring flood peak (May–June) that declined to a seasonal base flow by mid-summer to late-summer (Grams

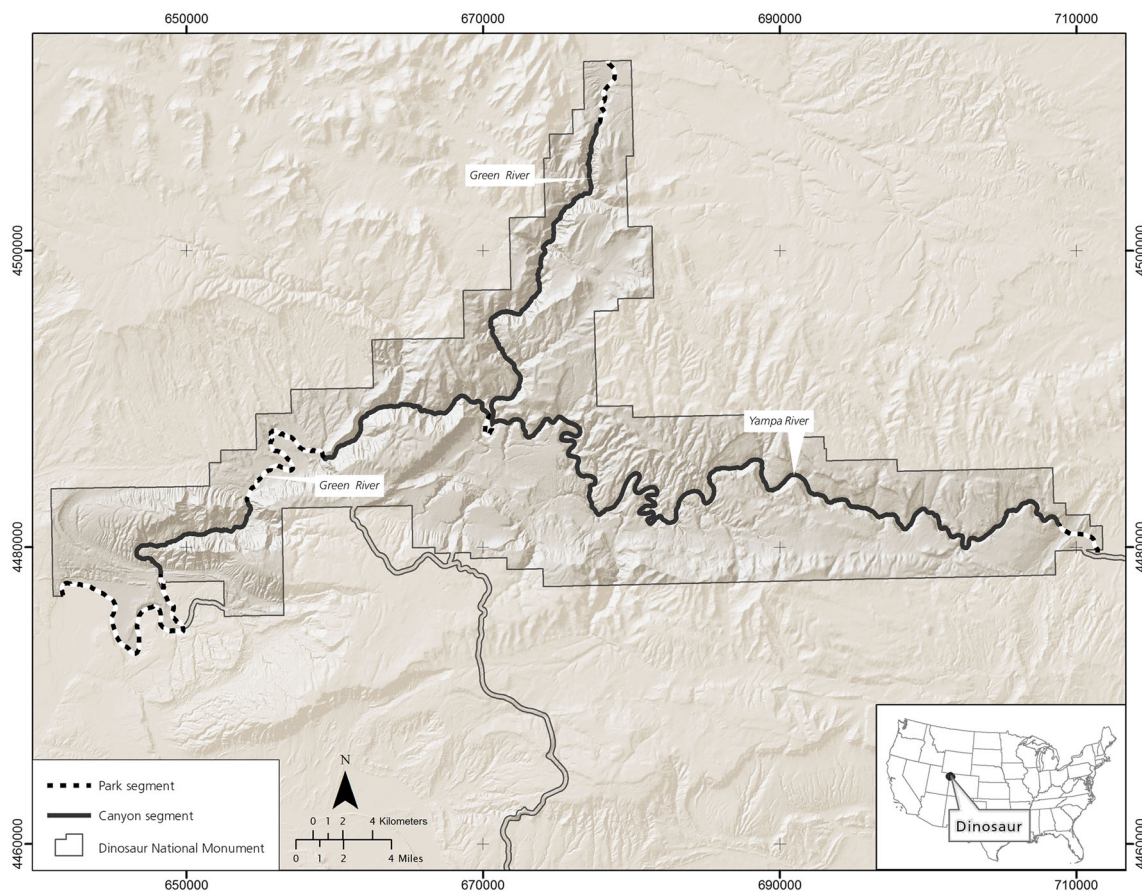


Figure 1. Areas monitored for invasive plants, in solid black, surveyed at Dinosaur National Monument on 5–24 July 2010 and 19–26 July 2011. This figure is available in colour online at wileyonlinelibrary.com/journal/trr

and Schmidt, 2005). Merritt and Cooper (2000) found that fluvial processes and riparian vegetation in alluvial parks, largely upstream of Dinosaur NM, were similar prior to regulation. Tamarisk arrived in the Green and Yampa River basins in approximately the 1930s to the 1940s (Allred and Schmidt, 1999; Cooper *et al.*, 2003; Manners *et al.*, 2014).

The hydrograph of the Yampa River reflects large inter-annual and intra-annual variability in annual peak flows and flow volume. Cooper *et al.* (1999) found that there has been no change in mean annual peak flows, and Manners *et al.* (2014) found no significant difference in total annual runoff or in the magnitude of the average 2-year recurrence flow between pre-dam and post-dam time periods. However, the hydrograph of the upper Green has been greatly altered following completion of Flaming Gorge Dam. The average 2-year recurrence flow has decreased 57% and 23% below Flaming Gorge Dam and on the lower Green River below the confluence with the Yampa River, respectively (Grams and Schmidt, 2002). At the same time, Flaming Gorge Dam operations have increased the upper and lower Green River base flows by approximately 220% and 230% of their pre-dam values (Cooper *et al.*, 1999). The Green River

channel has responded to reductions in peak flows by narrowing above the Yampa River confluence by 11% to 22% (Lyons *et al.*, 1992; Grams and Schmidt, 2002). The Yampa also narrowed over this time period, but to a lesser extent and in specific geomorphic settings. Manners *et al.* (2014) found that within Harding Hole and Laddie Park, two wider, entrenched meander reaches, the channel narrowed by 6% since 1961.

Invasive plant census

These methods are adapted from those developed by Dewey and Andersen (2004). We made a list of invasive plant species by reviewing literature and consulting with Dinosaur NM staff and county weed managers. These species were censused in canyon bound settings across the entire river bottomland within the study area (Figure 1). Areas where Dinosaur NM has conducted non-native plant removal (campgrounds and endangered fish habitat) were excluded from the census.

The minimum detection target size (MDTS) for invasive plants represented the patch size that was large enough to be

detected with a high level of confidence (>90%). We established a MDTs of 40 m² for all invasive plants. However, crews still recorded patches smaller than 40 m² when observed. The effective detection distance (EDD) was the maximum distance from which an observer could consistently detect the MDTs of the least-visible priority species. Using simulated plant patches of a targeted size, we tested crew members by determining the maximum distance from which they could consistently detect patches. We estimated the length of the EDD in the field either by pacing or using a laser rangefinder. The EDD was determined to be between 1 and 60 m, depending on vegetation type, density and observer. We considered non-native plant patches separated by more than 50 m to be distinct. If a patch was continuous for more than 50 m, patch size class estimates were made every 50 m.

While walking along the shore or floating on a raft, we searched for priority plant species. The areas searched generally covered all active bar surfaces, most of the active flood plain surface, and extended up into the inactive flood plain and upland terraces depending on the width of the bottomland. As the river corridors were traversed, locations of all priority species were recorded using global positioning system units with at least 5-m accuracy. Because it was so pervasive throughout the study area, cheatgrass (*Bromus tectorum*) was not mapped in this way.

For each priority species found, we recorded the size class of the patch according to the following criteria:

1. one to a few plants ($\leq 2 \times 2$ m);
2. few plants to 40 m²;
3. 40–400 m²;
4. 400–1000 m² and
5. 1000–2000 m².

Invasive plant sampling

We established vegetation transects perpendicular to the river channel at varying distances along alternating sides of the river, throughout each of the three study reaches. Where steep canyon walls or talus slopes prevented the establishment of transects, they were skipped. We systematically located 1-m² vegetation quadrats at 0.5, 5 and 10 m away from the water's edge along each transect and recorded per cent cover of all priority species using the following cover classes: <1%, 1% increments between 1% and 10% and 10% increments between 20% and 100%. Transect spacing was determined by the occurrence of invasive plants in quadrats along the sample transects. Initially, transects were established every 500 m along the channel within a river reach. If no invasive plants were detected in four consecutive transects, then spacing between transects was increased to 1000 m until plants were again detected and the 500 m spacing was resumed. Consequently, sampling intensity was higher in the Green River reaches where census results indicated higher densities and

larger patches of invasive plants. In all, a total of 53, 61 and 85 transects was established along the upper Green, lower Green and Yampa Rivers, respectively.

Comparisons to earlier surveys

Dewey and Andersen (2005)) surveyed the same sections of Dinosaur NM between 2002 and 2005. They sampled in approximately the same time period from May 28 to September 24. Fourteen species that were target species in 2002–2005 and priority species in 2010–2011 were detected in at least one of the two sampling periods. In the earlier surveys, crews generally mapped patches as points; however, many patches of tamarisk (68) along the upper Green and lower Green were mapped as a combination of points, lines and polygons, and two patches of sweetclover (*Melilotus officinalis*) along the lower Green were mapped as lines. In 2010 and 2011, points were used exclusively to map patches, with multiple points used if the patch occurred continuously along more than 50 m of the channel. Because of these methodological differences, comparisons could not be made between the two sampling periods for tamarisk or sweetclover on the Green River. Otherwise, the methods were comparable on the Yampa River and for all other invasive species.

Plant life history traits

We classified a number of plant life history traits that have been documented for the species that were found in our census, and which showed increases over the two sampling periods. Traits examined included longevity, dispersal characteristics, biotic interactions with other species, wetland indicator status and adaptations to disturbance. Information was derived primarily from the United States Department of Agriculture (USDA) plants database (USDA, NRCS 2015; <http://plants.usda.gov>, 12 September 2015) and AKEPIC (2015); <http://aknhp.uaa.alaska.edu/maps/akepic/>, 12 September 2015), an exotic plants database, and citations therein.

Analyses

We calculated the mean number of plant patches per hectare for each river reach. The area monitored was determined by multiplying the linear distance surveyed by the EDD. We calculated the mean and standard error of per cent cover by species from the quadrats. We used one-way analyses of variance to test for differences in total combined invasive plant mean cover and individual species mean cover across the three river reaches. If there was a difference, we used Tukey's honest significant difference test to identify where the differences were (R Core Team, 2014).

RESULTS

We detected a total of 14 invasive species using a census and sample quadrats, to examine 727 ha of bottomland along 171 river km in 2010–2011. A total of 2258 plant patches of 11 different species was detected within the study reaches. The upper Green River had the highest density of invasive plants (10.1 patches ha⁻¹) followed by the lower Green (4.4 per ha) and the Yampa (3.3 per ha). Tamarisk (2.9 patches ha⁻¹), Canada thistle (*Cirsium arvense*) (2.4 per ha), broadleaf pepperwort (*Lepidium latifolium*) (2.2 per ha) and sweetclover (1.5 per ha) all displayed the highest density of patches along the upper Green River (Figure 2). On the lower Green and Yampa Rivers, tamarisk was the only species with patch densities greater than 1.0 per ha (Figure 2). Patch densities by species were generally highest along the upper Green, followed by the lower Green, and were lowest on the Yampa (Figure 2).

Patches in the largest two size classes were generally higher on the upper and lower Green River than on the Yampa River for all species with >10 detections, except for Russian knapweed (*Centaurea repens*) where the largest patches were on the Yampa (Table 1). On the upper Green, 94% of the tamarisk patches were larger than 400 m², whereas on the lower Green and the Yampa, only 37% and 22% were larger than 400 m², respectively (Table 1).

We detected seven species in the quadrats along 199 transects sampled in 2010 and 2011 (Table 2). Invasive species were present in 23%, 19% and 4% of quadrats with an average

of 0.28, 0.22 and 0.04, invasive species occurrences per square metre along the upper Green, lower Green and Yampa rivers, respectively. Four species and all invasive plant species combined were detected in sufficient numbers to test for differences between the three river reaches. Total invasive species without tamarisk ($F=4.15$, $df=2$, $p=0.02$), tamarisk ($F=5.14$, $df=2$, $p=0.01$), cheatgrass ($F=4.54$, $df=2$, $p=0.01$) and Canada thistle ($F=2.16$, $df=2$, $p=0.02$) were all significantly different at the 0.05 level between the three river reaches (Table 2). For every test except cheatgrass, invasive species patches were significantly higher on the upper Green than either or both the lower Green and Yampa rivers, and no Canada thistle was sampled in quadrats on either the lower Green or Yampa. Cheatgrass per cent cover was higher on the lower Green than the upper Green or the Yampa. The Yampa River never had the highest per cent cover for any invasive species (Table 3).

Comparison to previous surveys

The total number of patches increased by 10%, 46% and 43% from the early sampling period (2002–2005) to the later sampling period (2010–2011) along the upper Green, lower Green and Yampa Rivers, respectively (Table 4). Sweetclover (+645%, 71 new patches on upper Green and +224%, 166 new patches on the Yampa) had some of the largest increases, although comparisons could not be made on the lower Green between the two time periods because of differences in methodology. Similarly, tamarisk increased by 25% (90 new patches) on the Yampa River but could not be compared with

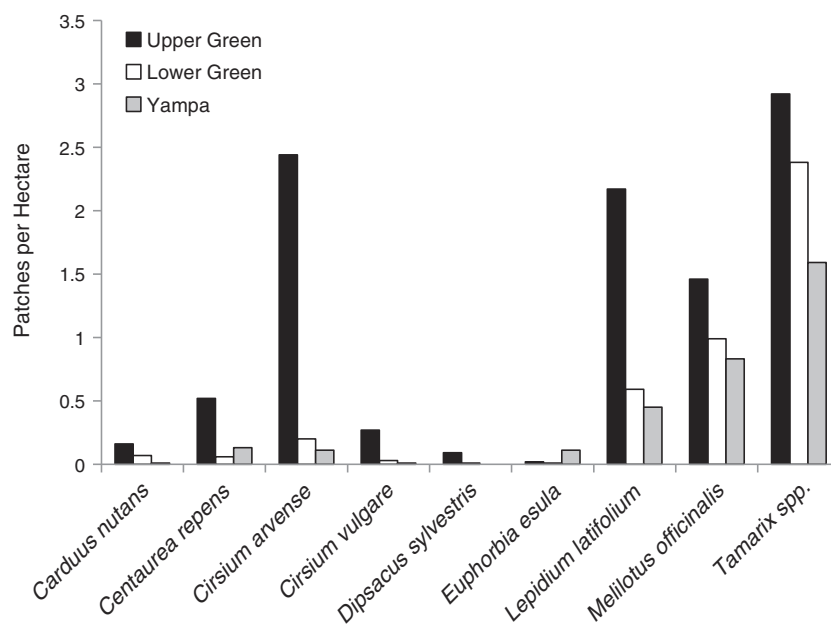


Figure 2. Number of non-native invasive plant patches per hectare along the Green River above the confluence (upper Green) (56.23 ha surveyed), the Green River below the confluence (lower Green) (173.31 ha surveyed) and the Yampa River (288.02 ha surveyed) at Dinosaur National Monument on 5–24 July 2010 and 19–26 July 2011. For species not listed, the patch density was <0.05 per ha.

Table I. Total patches observed, patch density (per hectare) and per cent occurrence by size class of eight priority non-native plant species patches, and all other priority species combined

Species	River	Total number of patches	Patch density	Size of invasive plant patches				
				One to few plants	Few plants to 40 m ²	40–400 m ²	400–1000 m ²	>1000 m ²
Bull thistle	UG	15	0.27	47%	53%	0%	0%	0%
	LG	5	0.03	20%	80%	0%	0%	0%
	YA	2	0.01	50%	50%	0%	0%	0%
Musk thistle	UG	9	0.16	44%	33%	22%	0%	0%
	LG	12	0.07	33%	25%	25%	17%	0%
	YA	3	0.01	67%	33%	0%	0%	0%
Leafy spurge	UG	1	0.02	0%	0%	100%	0%	0%
	LG	2	0.01	0%	0%	100%	0%	0%
	YA	31	0.11	19%	68%	13%	0%	0%
Russian knapweed	UG	29	0.52	3%	45%	34%	17%	0%
	LG	10	0.06	0%	60%	40%	0%	0%
	YA	38	0.03	5%	32%	34%	26%	3%
Canada thistle	UG	137	2.44	5%	26%	41%	27%	<1%
	LG	35	0.20	3%	34%	40%	23%	0%
	YA	33	0.11	15%	30%	45%	9%	0%
Broadleaf pepperwort	UG	123	2.17	9%	37%	27%	28%	0%
	LG	103	0.59	4%	21%	50%	24%	0%
	YA	129	0.45	9%	43%	36%	12%	0%
Sweetclover	UG	82	1.46	21%	39%	23%	16%	1%
	LG	171	0.99	11%	17%	54%	19%	0%
	YA	240	0.83	12%	38%	40%	9%	1%
Tamarisk	UG	164	2.92	1%	0%	5%	60%	34%
	LG	413	2.38	5%	8%	50%	34%	3%
	YA	457	1.59	28%	18%	33%	20%	2%
All other species	UG	6	0.10	67%	17%	17%	3%	0%
	LG	5	0.03	80%	20%	0%	0%	0%
	YA	3	0.01	100%	0%	0%	0%	0%

Percentages are given for each of the five size classes censused in 56 ha of bottomland along the upper Green (UG), 173 ha along the lower Green (LG) and 288 ha along the Yampa (YA) Rivers within Dinosaur National Monument on 5–24 July 2010 and 19–26 July 2011.

the two stretches of the Green River. Other notable increases by species included Russian knapweed (19 to 29 patches) on the upper Green River, broadleaf pepperwort (53 to 103

patches) on the lower Green River, and Canada thistle (four to 33 patches) and leafy spurge (*Euphorbia esula*) (11 to 31 patches) on the Yampa River. Broadleaf pepperwort (144 to

Table II. Number of monitoring transects where non-native plant species were detected, mean per cent cover, standard error by sampling area and results of one-way analyses of variance to test for differences in cover of invasive non-native plants across three river reaches: the upper Green, lower Green and Yampa Rivers in the Dinosaur National Monument (July 2010 and 2011)

Species	Upper Green (53)		Lower Green (61)		Yampa (85)		Sum of squares	df	Mean square	F-ratio	p
	Number	cover (SE)	Number	cover (SE)	Number	cover (SE)					
Cheatgrass	0	0.00 (0.00)	24	0.28 (0.12)	1	0.04 (0.04)	2.79	2	1.39	4.54	0.01**
Russian knapweed	2	0.16 (0.13)	0	0.00 (0.00)	0	0.00 (0.00)			Not tested		
Canada thistle	7	0.33 (0.20)	0	0.00 (0.00)	0	0.00 (0.00)	4.32	2	2.16	3.88	0.02*
Broadleaf pepperwort	6	0.43 (0.38)	0	0.00 (0.00)	0	0.00 (0.00)	7.22	2	3.61	1.80	0.17
Sweetclover	0	0.00 (0.00)	2	0.01 (<0.01)	2	0.02 (0.02)			Not tested		
Tamarisk	29	3.40 (1.03)	15	1.45 (0.67)	6	0.54 (0.29)	269.00	2	134.48	5.14	0.01**
Total no. of Tamarisk	12	0.92 (0.43)	24	0.28 (0.12)	3	0.06 (0.04)	24.66	2	2.97	4.15	0.02*

Total number of transects per sampling route are listed in parentheses in the header row. Asterisks * and ** are equal to significant and highly significant statistical differences, respectively.

SE, standard error.

Table III. Results of Tukey's honest significant difference test to determine how differences in mean per cent cover, as sampled in quadrats, were distributed among invasive non-native plants along the upper Green, lower Green and Yampa Rivers at Dinosaur National Monument

Species	Mean % cover	Standard deviation	n	Tukey
Canada thistle				
Upper Green	0.33	1.45	53	A
Lower Green	0.00	0.00	61	B
Yampa	0.00	0.00	85	B
Cheatgrass				
Upper Green	0.00	0.00	53	A
Lower Green	0.28	0.91	61	B
Yampa	0.04	0.36	85	A
Tamarisk				
Upper Green	3.40	5.22	53	A
Lower Green	1.45	7.48	61	AB
Yampa	0.54	2.63	85	B
All priority IEP without Tamarisk				
Upper Green	0.92	3.16	53	A
Lower Green	0.28	0.91	61	AB
Yampa	0.06	0.40	85	B

IEP, invasive exotic plant

Sampling occurred in July of 2010 and 2011. Different letters denote significant between-group differences at the 0.05 level.

122 patches) and Canada thistle (57 to 35 patches) on the upper Green River were the only species on any river reach with more than 20 patches that decreased from the early sampling period to the later sampling period (Table 4).

DISCUSSION

Because flow regulation is so pervasive, it is often difficult to isolate the effects of regulation on riparian plant invasions from other factors such as climate variation and differences in fluvial geomorphic setting and processes. We took advantage of the fact that where the largely unregulated Yampa

River joins the highly regulated Green River, a partially regulated reach of the Green River results below this confluence. These three reaches, with distinctly different degrees of regulation, are set within the bedrock canyons of Dinosaur NM, where pre-regulation hydrology, geomorphic setting and processes, land use and riparian vegetation were broadly similar. This rather unique set of conditions provided a natural experiment where the role of flow regulation in the invasion of several important non-native riparian plants could be examined with a minimum of complicating factors (cf. *Manners et al.*, 2014).

Results of this study support the findings of others that have used unpaired river reaches to demonstrate that tamarisk is more abundant along regulated rivers when compared with unregulated rivers (*Stromberg et al.*, 2007b). We found that tamarisk on the highly regulated upper Green River had higher patch densities and the greatest percentage of large patch sizes (Table 2) along with significantly higher mean per cent cover values, compared with the less regulated Green and lightly regulated Yampa Rivers (Tables 2 and 3). This finding is consistent with the observation that tamarisk dominance was greatest on the most regulated rivers (Merritt and Poff 2010). Our results further demonstrate that this pattern of increasing patch density and patch size is not limited to tamarisk but holds for other invasive herbaceous species, including Canada thistle and broadleaf pepperwort (Table 1). When all priority invasive species (minus tamarisk) were combined, the total mean per cent cover, like tamarisk, was significantly different across the three reaches, with the highest covers in the highly regulated reach and the lowest in the least regulated reach (Table 2 and 3).

Studies on tamarisk may provide more general insights into how the invasion process for this species is influenced by flow regulation. In a study of tamarisk in Dinosaur NM, Larson (2004) found that the percentage of available habitat occupied by tamarisk declined as mean unit stream power increased. This suggests that low energy hydrologic

Table IV. Priority species observed and number of patches for non-native invasive species with more than 10 detections in both sampling periods detected along the upper Green River, lower Green River and Yampa River at Dinosaur National Monument on 5–24 July 2010 and 19–26 July 2011, compared with data collected from May to September 2002 to 2005, along the same census route

Species	Number of patches								
	Upper Green River			Lower Green River			Yampa River		
	2002–2005	2010–2011	Change	2002–2005	2010–2011	Change	2002–2005	2010–2011	Change
Musk thistle	16	9	–43%	0	12	+	1	3	+200%
Russian knapweed	19	29	+53%	1	10	+900%	28	38	+36%
Canada thistle	94	137	+46%	57	35	–39%	4	33	+725%
Bull thistle	16	15	–6%	2	5	+150%	2	2	0%
Leafy spurge	0	1	+	5	2	–60%	11	31	+182%
Broadleaf pepperwort	144	122	–15%	53	103	+94%	114	129	+13%
All spp. (no tamarisk/sweetclover)	290	320	+10%	118	172	+46%	167	239	+43%

Table V. Summary of life history traits for eight priority regional weeds found within the study area

Species name	Common name	Vegetative reproduction	Lifespan	Wetland indicator status	Allelopathic	Seed dispersal	Spreading root system (rhizomes, etc.)	Can form dense stands or monocultures	Disturbance adapted
<i>Acroptilon repens</i>	Russian knapweed	Yes	Perennial	Not listed	Yes	Human	Yes	Yes	Yes
<i>Cirsium arvense</i>	Canada thistle	Yes	Perennial	FACU	Yes	Wind, water, animal and human	Yes	Yes	Yes
<i>Lepidium latifolium</i>	Broadleaf pepperwort	Yes	Perennial	FAC	Not reported	Wind, water and human	Yes	Yes	Not reported
<i>Cirsium vulgare</i>	Bull thistle	No	Biennial	FACU	Not reported	Wind and human	No	Yes	Yes
<i>Euphorbia esula</i>	Leafy spurge	Yes	Perennial	Not listed	Yes	Wind, water, animal and human	Yes	Yes	Yes
<i>Carduus nutans</i>	Musk thistle	No	Biennial/perennial	FACU	Possibly	Wind, water, animal and human	No	Yes	Yes
<i>Melilotus officinalis</i>	Sweetclover	No	Annual/biennial/perennial	FACU	Yes	Water and human	No	Yes	Yes
<i>Tamarix</i> spp.	Tamarisk	No	Perennial	FAC	Not established	Wind, water and human	No	Yes	Yes

Information on species derived primarily from the USDA plants database (USDA, NRCS 2015; <http://plants.usda.gov>, 12 September 2015) and AKEPIC (2015); <http://aknbp.uaa.alaska.edu/maps/akepic/>, 12 September 2015), an exotic plants database, and citations therein. FACU, facultative upland; FAC, facultative.

environments on relatively unregulated rivers like the Yampa are prone to invasion, and further, such low energy environments may expand during periods of climate-related reductions in flow, or be made available on higher surfaces during large flood years. Consistent with this, Manners *et al.* (2014) found that tamarisk on the Yampa River established both during periods of low flows and high flows, although the large majority of individuals established below the average 2-year return flood. Thus, along largely unregulated rivers, successful invasions of tamarisk can be initiated by low flows on normally active channel surfaces during climatically induced dry periods and by large flows on flood plain surfaces. Although invasive, non-native herbs cannot be directly aged after the fact to determine year of establishment, their life history traits (Table 5) and the type of surface upon which they were established can provide clues to how and when they may have established as well as how likely they are to expand and persist.

Flow regulation can be viewed as an extreme and persistent form of climate-induced low flows where extensive unvegetated channel bedforms and low energy hydrologic environments represent fundamentally new habitats. In contrast, the majority of tamarisk found along the heavily regulated upper Green River established and persisted on alluvial surfaces that formed immediately prior to and following completion of Flaming Gorge Dam (Larson, 2004; Alexander, 2007). These new post-dam surfaces allowed for the rapid expansion of an early successional species like tamarisk (Alexander, 2007). Although tamarisk was present in Lodore Canyon in the pre-dam period, river regulation has provided novel and favourable environmental conditions for the expansion of this species (Cooper *et al.*, 2003) and likely explains why tamarisk dominance is highest on regulated rivers (Merritt and Poff, 2010). This may also account for increases in the numbers and sizes of some of the invasive herb patches on the highly regulated reach examined in this study. Once established, the growth and persistence of an invasive patch would be important information and relevant to the question of whether an invasive species is altering native species assemblages (Tickner *et al.*, 2001). For example, a species like Canada thistle, which is a rhizomatous perennial with apparent allelopathic properties (Stachon and Zimdahl, 1980), could persist, expand at the expense of native species and serve as a seed source for further recruitment.

Results of invasive plant sampling from the 2002–2005 to the 2010–2011 time period indicate that for herbaceous species, the upper Green River showed a modest increase in species numbers compared with greater than 40% increases for both the lower Green and Yampa (Table 5). This may relate to the stable post-dam hydrograph of the upper Green River and establishment of vegetation on most of the available post-dam surfaces by 2002–2005. In contrast, ongoing fluvial disturbances and high flow variability along the Yampa and lower Green Rivers continue to dynamically create new opportunities

for establishment and persistence of invasive species. Temporal patterns for individual species were variable, showing overall increases (Russian knapweed) or gains in some reaches and losses in others (Canada thistle), but in general, species like broadleaf pepperwort, which successfully invades wetlands and riparian ecosystems, often forming monotypic stands (Blank and Young, 2002), along with musk thistle (*Carduus nuttans*), show consistent increases in the less regulated reaches (Table 4). This raises the question, is the invasion processes just slower in less regulated reaches? Richardson *et al.* (2007) present a hypothetical scenario in which successive, large flood events promote eventual dominance by an invasive species with progressive loss of native community structure and resilience.

Using large, international datasets, Catford and Jansson (2014) indicate that from a regional species pool, successful non-native invaders of riparian zones generally have higher seed availability and dispersal potential, often occupy higher, drier locations within the riparian zone and are adapted to or tolerant of flood disturbance, which may also reduce competitive interactions. Examination of the life history traits of many of the invasive, non-native herb species in the study is consistent with these findings. Specifically, we found that these species are generally dispersed by a number of mechanisms including water and human activities, are adapted to establishing following disturbance, are competitive perennials that often form dense monocultures and occur in both wetland and upland landscape settings (Table 5). Although it appears that flow regulation may have influenced the timing and extent of invasion by many of these non-native species, because of their life history traits, these species are likely to continue to invade and persist to some degree in riparian settings regionally, regardless of the degree of flow regulation. For example, because many of these invasive species are associated with human activities like grazing and agriculture (AKEPIC 2015) and such activities are common on river flood plains, riparian zones are subject to continual inputs of propagules. As has been shown with some non-native, woody riparian invasions, flow regulation alone is likely not the only factor driving invasions of certain non-native herbs. Future monitoring and management of invasive species in riparian ecosystems would benefit by including knowledge of key life history traits, hydrological variables and site-scale distribution along physical environmental gradients (Mortenson and Weisberg, 2010; Catford and Jansson, 2014).

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